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^{14}C DATES AND STABLE ISOTOPE ECOLOGY OF MARINE VERTEBRATES IN THE LATE PLEISTOCENE-EARLY HOLOCENE CHAMPLAIN SEA

Robert S Feranec[1]* • Mario E Cournoyer[2] • Andrew L Kozlowski[1]

[1]New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, USA
[2]Musée de paléontologie et de l'évolution, 541 de la Congrégation, Montréal, QC H3K 2J1, Canada

ABSTRACT. The late Pleistocene to early Holocene Champlain Sea provides a unique opportunity to study the development of marine ecosystems in a context of global climatic change. This study presents radiocarbon (^{14}C) dates and stable isotope analyses on 15 vertebrate specimens from Champlain Sea sediments, including the Charlotte Whale, which is Vermont's State marine fossil. Data are used in an attempt to investigate the timing of colonization and ecological dynamics in this newly formed sea. Using the average marine correction, ^{14}C dates on four specimens likely calibrate prior to or possibly synchronous with the accepted origination date for the Champlain Sea, implying larger marine reservoir effects than the average marine correction in the vertebrate tissues. Without knowing the specific marine reservoir offsets, it is not possible to calculate the timing of colonization or its relation to concurrent climatic change. Observed lower δ^{13}C and δ^{15}N values in walruses, a fin whale, and a right whale support consumption of prey from lower trophic levels such as bivalve mollusks, krill, and copepods. Higher isotopic values in beluga whales and a bird, the thick-billed murre, support consuming fish, such as cod and capelin. These isotopic data show comparable values and relationships as observed in modern arctic marine ecosystems.

KEYWORDS: Champlain Sea, chronology, paleoecology, Pleistocene, vertebrates.

INTRODUCTION

The Champlain Sea (CS), North America's most recent inland sea, occurred in the St. Lawrence Lowland covering parts of the northeastern United States and southeastern Canada from about 13,000 to 10,600 cal BP (Figure 1) (Occhietti 2007; Cronin et al. 2008), that is from about 11,100 to 9500 ^{14}C yr BP. Isostatic depression caused by the enormous weight of the Laurentide Ice Sheet (LIS) depressed the area leaving the St. Lawrence Lowland below sea level. Subsequent northward retreat of the LIS allowed the Atlantic Ocean to flood this then-below-sea-level area until the region rebounded, and seawaters retreated eastward. Sedimentological evidence shows a clear transgression-regression cycle and the transition from terrestrial to marine and back to terrestrial habitats (Gadd 1988; Prichonnet 1988; Cronin et al. 2008; Rayburn et al. 2011; Belrose 2015; Normandeau et al. 2017). These sediments are also known to contain an abundant diversity of marine and terrestrial/lacustrine invertebrate and vertebrate fossils, including taxa such as bivalve mollusks, fishes, and whales (Harington 1977; Harington 1988; McAllister et al. 1988; Harington 2003a; Harington et al. 2006; Feranec et al. 2014).

Establishment of the CS could present a unique opportunity to study aspects of how marine ecosystems develop themselves anew. Additionally, detailed studies of this ecosystem may be informative with respect to the responses of marine animals to on-going climatic change as the CS spanned a period of intense global warming at the Pleistocene-Holocene transition (Cronin et al. 2008; Steffensen et al. 2008). Here, we present radiocarbon (^{14}C) and stable isotope data from a set of marine vertebrates (i.e., mammal and bird) from different localities across the CS with the aim of determining (1) the timing of colonization by particular fauna and if certain taxa colonize before others, (2) whether the Champlain Sea marine ecosystem was different from modern ecosystems containing similar species, and (3) what the fauna imply about specific habitats in the Champlain Sea.

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*Corresponding author. Email: robert.feranec@nysed.gov

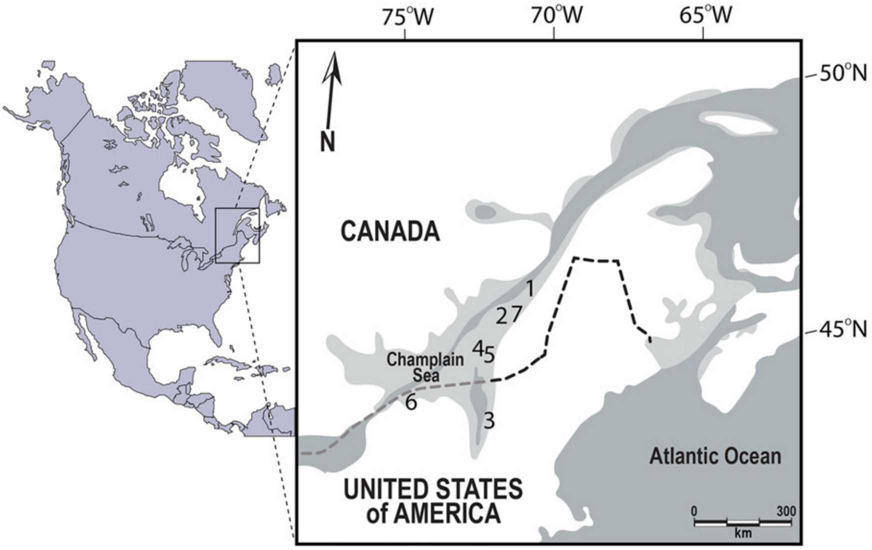

Figure 1 Map of the location and extent of the Champlain Sea overlaying present-day geography. On inset, dark gray represents current waterways while light gray represents land inundated by water during the extent of Champlain Sea. Numbers refer to location of fossil specimens presented in this study as follows: 1, Saint-Nicolas, Québec, Canada; 2, Daveluyville, Québec, Canada; 3, Charlotte, Vermont, USA; 4, Mont-Saint-Hilaire, Québec, Canada; 5, Saint-Césaire, Québec, Canada; 6, Norfolk, NY, USA; 7, Plessisville, Québec, Canada.

Timing the colonization of the CS requires knowing the age of its inception. Inundation of the St. Lawrence Lowland by marine waters is of course dependent on geography and geomorphology and likely not synchronous for all locations. Sites nearer the mouth of the St. Lawrence necessarily would be flooded earlier than sites to the west. While this commencement date has occasionally been reported using dates from mollusks which might be affected by marine reservoir effects (Rodrigues 1988; Parent and Occhietti 1999; England et al. 2013), Richard and Occhietti (2005) present an age of 11,100 ± 100 ^{14}C yr BP (12,770–13,170 cal BP) based on a terrestrial plant date and the regression rate of the LIS at Québec, Canada. This calibrated age range for the onset of the CS has been supported by additional studies (Rayburn et al. 2007; Cronin et al. 2008; Rayburn et al. 2011).

The waxing and waning of marine waters in the CS also resulted in changes to marine habitats at particular locations over time. Factors such as isostatic rebound, influx of meteoric and/or glacial meltwater, and the geomorphology and depth of the site, for example, would affect what fauna could survive at a particular place and time (Hillaire-Marcel 1988). Recognizing this variability in marine habitats over time, this study, in part, explores whether vertebrate ecology in the CS was similar to or different from the known modern ecology of the same species.

^{14}C dates on bone collagen have long been used to ascertain the ages of fauna from the CS (Dyck et al. 1966; Harington 1977; Lowdon and Blake 1981; Harington 1988; Harington 2003a, 2003b; Feranec et al. 2014). Similarly, the analysis of stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values has been well established as a technique to understand the ecology and ecological relationships of marine fauna (Fry and Sherr 1989; Fry and Wainright 1991; Hobson and Welch 1992; Clementz and Koch 2001; Newsome et al. 2010). The stable isotope analyses in this study are expressed in standard δ-notation: $X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is the δ^{13}C or δ^{15}N value, and $R = {}^{13}C/{}^{12}C$ or

$^{15}N/^{14}N$, respectively. $\delta^{13}C$ values are reported relative to the V-PDB standard, and $\delta^{15}N$ values are reported relative to atmospheric N_2. Bone collagen $\delta^{13}C$ values derive from the individual's diet and variation in the values is largely controlled by primary producers at the base of food webs (Fry and Sherr 1989; Koch 1998; Clementz and Koch 2001; Newsome et al. 2010). In terrestrial ecosystems, photosynthetic pathway (i.e., C_3, C_4, or CAM), primarily controls stable carbon isotope values, with C_3 having the lowest values, C_4 the highest, and CAM in between (O'Leary 1988; Ehleringer and Monson 1993; Koch 1998). In marine ecosystems, primary producers show a very wide range of $\delta^{13}C$ values (Fry and Sherr 1989). Factors controlling these values include the concentration of dissolved CO_2 and HCO_3^-, and differences in productivity, for example (Fry and Sherr 1989; Clementz and Koch 2001). Differences in productivity can also lead to geographic differences in the $\delta^{13}C$ values of primary producers in nearshore versus offshore habitats (Burton and Koch 1999; Clementz and Koch 2001; Newsome et al. 2010). Nearshore habitats generally have higher productivity, and thus primary producers having higher $\delta^{13}C$ values than offshore habitats. However, this relationship can be complicated in nearshore glacial settings as the influx of meltwater can affect salinity, pCO_2, and temperature, for example, all factors that would influence $\delta^{13}C$ values at the base of marine food webs (Hillaire-Marcel 1988; Rau et al. 1989, 1991; Clementz and Koch 2001; Anderson et al. 2007; Cronin et al. 2008; Xiao et al. 2011; Calleja et al. 2017).

$\delta^{15}N$ values generally relate to trophic level, with higher values being found in individuals feeding higher in the food chain (Peterson and Fry 1987; Fry and Sherr 1989; Hobson and Welch 1992; Newsome et al. 2010). We expect primary producers to have the lowest $\delta^{15}N$ values and apex predators to have the highest (Peterson and Fry 1987; Fry and Sherr 1989; Hobson and Welch 1992; Van der Zanden and Rasmussen 1999; Clementz and Koch 2001; Newsome et al. 2010).

METHODS

Fifteen specimens representing 12 individuals of CS vertebrates were analyzed. Species include the following: *Uria lomvia* (thick-billed murre bird), *Odobenus rosmarus* (walrus), *Balaenoptera physalus* (fin whale), *Delphinapterus leucas* (beluga whale), and right whale (*Eubalaena cf. glacialis*). These specimens are housed in three different institutions: the Musée de paléontologie et de l'évolution (MPE; Montréal, Canada), the New York State Museum (NYSM; Albany, NY, USA), and the Perkins Museum of Geology (University of Vermont, Burlington, VT, USA). Samples were taken from museum specimens and submitted to the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at U.C. Irvine, Irvine, CA, USA (UCIAMS) for both radiocarbon and stable isotope analyses. Sample processing at the UCIAMS follows standard procedures for extracting bone collagen and can be found in more detail in Beaumont et al. (2010), and on the laboratory's website (UCIAMS 2021). Generally, UCIAMS uses a modified Longin (1971) method for collagen extraction (Brown et al. 1988). Generally, the bone samples are first decalcified with acid, then treated with a weak base to extract possible contaminating humics, and finally the remaining organic collagen is hydrolyzed to gelatin at 60°C in a weak acid. Afterwards, the gelatin solution is filtered to remove any remaining solids, and then ultra-filtered to remove the 30 kD fraction, which is then lyophilized. This freeze-dried sample is then graphitized and analyzed for ^{14}C.

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope data were obtained on splits of the bone collagen. These samples were analyzed separately on a Fisons NA1500NC elemental analyzer/Finnigan Delta Plus isotope ratio mass spectrometer. The $\delta^{13}C$ and $\delta^{15}N$ values have a precision of <0.1‰ and <0.2‰, respectively.

RESULTS

Radiocarbon Dates

The newly acquired radiocarbon dates range from 9965 ± 35 ^{14}C yr BP for the thick-billed murre bird (*Uria lomvia*) to 11,930 ± 30 ^{14}C yr BP in one of the fin whale (*Balaenoptera physalis*) specimens (Table 1). We highlight dates from two individuals (four specimens) below due to their historical significance.

Beluga Whale, *Delphinapterus leucas* (Charlotte, Chittenden County, Vermont, USA); The Charlotte Whale—The Vermont State Marine Fossil

UCIAMS 190567. **^{14}C yr BP 11640 ± 35**
$\delta^{13}C = -13.1‰$

Bone collagen. Sample taken from ventral side of the 7th lumbar vertebra of the Charlotte Whale.

Comments: A beluga whale was discovered in August 1849 during excavation of the Rutland and Burlington (Vermont, USA) railroad. The bones were found in blue clay about 8 feet (~2.4 m) below the present-day surface. The bones were given to Zadock Thompson, a noted scientist of Vermont's natural history, by engineers of the railroad. Upon receiving the bones, and to prevent crumbling, Thompson immersed them in "animal glue" (Thompson 1853). Thompson identified the specimen as a beluga whale, and later received confirmation of that diagnosis from Louis Agassiz of Harvard University (Cambridge, MA, USA). The stable isotope analyses on this specimen are similar to the other beluga whales included in this study (Table 2). This specimen was designated as Vermont's state fossil in 1993. In 2014, the designation was amended that this specimen is Vermont's state marine fossil. The Mount Holly Mammoth (*Mammuthus primigenius*), discovered by the same railroad company in 1848, was then designated as the State's terrestrial fossil.

Fin Whale, *Balaenoptera physalus* (Daveluyville, Québec, Canada); the Daveluyville Whale

UCIAMS 182297. MPEP578.1 **^{14}C yr BP 11770 ± 30**
$\delta^{13}C = -14.7‰$

Bone collagen. Sample taken from a vertebra of the Daveluyville Whale. MPEP578.1 was previously dated to 11,400 ± 90 ^{14}C yr BP (GSC-2871) using a 760g vertebra bone core sample (sample CR-78-21; Lowdon and Blake, 1981), and this date was assigned for the whole Daveluyville Whale skeleton.

UCIAMS 182296. MPEP717.109 **^{14}C yr BP 11840 ± 30**
$\delta^{13}C = -14.6‰$

Bone collagen. Sample taken from a bone fragment of the Daveluyville Whale.

UCIAMS 182298. MPEP717.2 **^{14}C yr BP 11930 ± 30**
$\delta^{13}C = -14.6‰$

Bone collagen. Sample taken from the left mandible of the Daveluyville Whale.

Table 1 Locality information, fraction modern, conventional ^{14}C date, calibrated ^{14}C date, and calibrated date with marine reservoir offset correction from Champlain Sea fossils newly analyzed in this study.

UCIAMS	Museum no.	Locality[a]	Fraction Modern	^{14}C yr BP	Marine20 Calibration (cal BP; 2σ)	Marine20 Calibration with ΔR[b] (cal BP)
Birds						
Thick-billed Murre (*Uria lomvia*)						
190573	MPEP34.1	(1)	0.2892 ± 0.0011	9965 ± 35	11060–10640	10320–8960
Mammals						
Walrus (*Odobenus rosmarus*)						
185703	MPEP44.4	(1)	0.2706 ± 0.0010	10500 ± 30	11780–11340	11060–9600
185706	MPEP80.1	(1)	0.2609 ± 0.0010	10795 ± 35	12310–11810	11480–9990
190571	MPEP87.1	(1)	0.2606 ± 0.0011	10805 ± 35	12320–11820	11500–10010
182292	MPEP577.1	(1)	0.2687 ± 0.0008	10555 ± 25	11860–11430	11140–9670
185701	MPEP577.1	(1)	0.2690 ± 0.0010	10545 ± 30	11840–11500	11120–9660
Fin Whale (*Balaenoptera physalus*)						
182297	MPEP578.1	(2)	0.2310 ± 0.0008	11770 ± 30	13240–12930	12710–11350
182296	MPEP717.109	(2)	0.2291 ± 0.0008	11840 ± 30	13310–13020	12760–11400
182298	MPEP717.2	(2)	0.2265 ± 0.0008	11930 ± 30	13400–13100	12900–11550
Beluga Whale (*Delphinapterus leucas*)						
190567	Charlotte Whale	(3)	0.2348 ± 0.0010	11640 ± 35	13100–12800	12610–11210
190572	MPEP51.1	(1)	0.2686 ± 0.0011	10560 ± 35	11870–11420	11140–9680
182293	MPEP859.1	(4)	0.2769 ± 0.0008	10315 ± 25	11480–11150	10810–9390
182295	MPEP911.1	(5)	0.2786 ± 0.0009	10265 ± 25	11390–11090	10720–9330
225606	NYSM VP-5095	(6)	0.2482 ± 0.0010	11195 ± 35	12700–12430	12080–10510
Right Whale (*Eubalaena cf. glacialis*)						
182294	MPEP913.1	(7)	0.2318 ± 0.0009	11745 ± 35	13220–12900	12690–11320

[a] Locality: 1, Saint-Nicolas, Québec, Canada; 2, Daveluyville, Québec, Canada; 3, Charlotte, Vermont, USA; 4, Mont-Saint-Hilaire, Québec, Canada; 5, Saint-Césaire, Québec, Canada; 6, Norfolk, NY, USA; 7, Plessisville, Québec, Canada.

[b] Marine reservoir effect (ΔR) of 900 ± 262 from Richard and Occhietti (2005) using the Marine20 calibration in Calib 8.1.

Table 2 Stable isotope values of Champlain Sea fossils.

UCIAMS	Museum no.	%C	$\delta^{13}C_{pdb}$ (‰)	%N	$\delta^{15}N_{air}$ (‰)	C/N
Birds						
Thick-billed Murre (*Uria lomvia*)						
190573	MPEP34.1	40.8	–14.7	14.5	18.9	3.28
Mammals						
Walrus (*Odobenus rosmarus*)						
185703	MPEP44.4	44.0	–14.5	16.0	12.2	3.21
185706	MPEP80.1	43.3	–15.2	15.7	12.0	3.22
190571	MPEP87.1	42.7	–15.0	15.3	10.9	3.26
182292	MPEP577.1	39.7	–13.8	14.5	12.2	3.20
185701	MPEP577.1	43.3	–14.4	15.6	12.5	3.25
Fin Whale (*Balaenoptera physalis*)						
182297	MPEP578.1	41.6	–14.7	15.3	12.4	3.16
182296	MPEP717.109	41.9	–14.6	15.1	13.0	3.24
182298	MPEP717.2	42.3	–14.6	15.0	12.9	3.30
Beluga Whale (*Delphinapterus leucas*)						
190567	Charlotte Whale	40.2	–13.1	14.4	18.1	3.25
190572	MPEP51.1	40.9	–14.2	14.4	18.6	3.32
182293	MPEP859.1	40.9	–13.8	14.9	17.8	3.20
182295	MPEP911.1	39.6	–12.8	14.6	18.7	3.16
225606	NYSM VP-5095	43.1	–13.3	15.8	16.9	3.2
Right Whale (*Eubalaena cf. glacialis*)						
182294	MPEP913.1	42.8	–15.1	15.4	12.3	3.26

Comments: In 1947, the nearly complete skeleton of the Daveluyville Whale was recovered from clay sediments about 3.6 km southwest of Daveluyville, Québec, Canada (Harington 1977). The remains of this specimen are now housed in the Musée de paléontologie et de l'évolution (Montréal, Canada), having previously been housed in a museum in Trois-Rivières (Québec, Canada) in the 2000s, and before that in its original exhibition at the Université du Québec à Trois-Rivières (UQTR), from the late 1970s to early 1990s. This specimen is catalogued under accession number MPEP717 which includes 127 fragmentary to complete bones. Amongst these bones are a partial left posterior skull, a partial left mandible, the proximal part of right mandible, left scapula, right ulna, several ribs, several vertebrae, and many partial bones and bone fragments. Examination of the vertebrae of MPEP717 shows that the epiphyseal plates are not fused indicating that this specimen is likely a juvenile/sub-adult individual. The presence of unfused vertebrae is supported by examination of an early picture of the whale skeleton (i.e., Fig. 2 in Laverdière 1950). Another specimen, a lone vertebra (MPEP578.1), ascribed as belonging to the Daveluyville Whale, differs from the other vertebrae for this individual in that its epiphyseal plates are fused. As noted above, this specimen was radiocarbon dated and the date was ascribed to the whole skeleton (Lowdon and Blake, 1981). Because of the lack of fused vertebrae in MPEP717 and the fact that MPEP578.1 is fused, it would appear that MPEP578.1 does not represent the same individual as the specimens of MPEP717. The three dates obtained here are statistically significantly different from each other ($t(2) = 14.2963$, $p < 0.003$), with the date from the mandible being significantly older than the other two. These three new dates are also statistically significantly older than the previously obtained date from MPEP578.1 (GSC-2871; Lowdon and Blake 1981), although the three most recent ^{14}C dates, that is UCIAMS 182296, UCIAMS 182297,

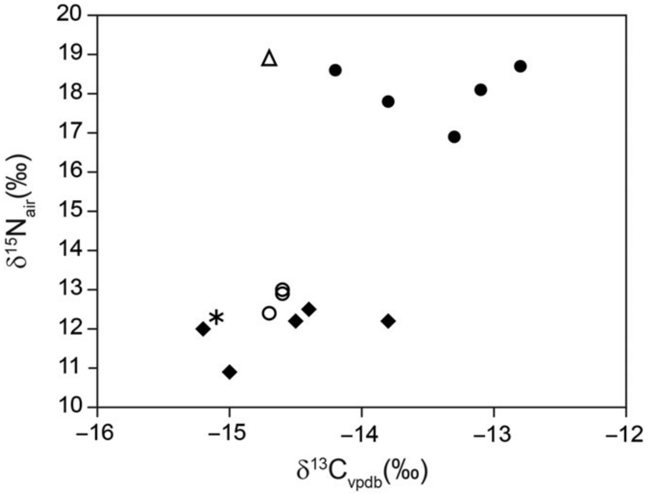

Figure 2 Stable carbon and nitrogen isotope values from specimens analyzed in this study. Symbols: black diamonds, walruses; black circles, beluga whale; open circles, fin whale; asterisk, right whale; open triangle, thick-billed murre.

and UCIAMS 182298, are close enough that the statistical differences among the dated elements may not be meaningfully different in terms of the actual age of when this individual died.

Stable Isotope Analyses

Stable isotope data are presented in Table 2 and Figure 2. The δ^{13}C values for all individuals appear similar, ranging from –12.8‰ to –15.2‰, although when species with only a single individual are excluded from the dataset a statistically significant difference is observed between the beluga whales ($\bar{X}$ = –13.4‰, $\sigma = 0.6$‰) and walruses ($\bar{X}$ = –14.6‰, $\sigma = 0.5$‰) with belugas showing slightly higher values (t(8) = –3.251, $p < 0.012$).

For δ^{15}N values, there does appear to be differences among individuals. The total range for all specimens in this study extends from 10.9‰ to 18.9‰, but there appears to be two populations of values, those below 14‰ and those above 16‰. The fin whale, right whale, and walruses show lower δ^{15}N values, while the belugas and thick-billed murre have higher values. Again, when species with only a single individual are excluded from the analysis, a statistically significant difference is observed between the beluga whales ($\bar{X} = 18.0$‰, $\sigma = 0.7$‰) and walruses ($\bar{X} = 12.0$‰, $\sigma = 0.6$‰), with belugas showing higher values (t(8) = –14.205, $p < 0.0001$).

DISCUSSION

Calibration of the dates using the Marine20 calibration curve places some of the older ^{14}C-dated vertebrate specimens, that is, the Charlotte Whale, the Daveluyville Whale, and the right whale, beyond or just synchronous with the earliest date recognized for the inception of the CS (i.e., about 13,000 ± 200 cal BP) (Occhietti and Richard 2003; Richard and Occhietti 2005; Rayburn et al. 2007; Cronin et al. 2008; Rayburn et al. 2011; Heaton et al. 2020; Reimer et al. 2020). The use of "animal glue" to preserve the Charlotte Whale might cause hesitation in accepting the ^{14}C date as accurate for this specimen, but the glue should pull the date to the more recent, not older (Thompson 1853; Takahashi et al. 2002). As was done for this specimen, a simple wash in distilled water and the standard preparation of bone collagen provides adequate removal of the animal glue for stable isotope analyses (Takahashi et al. 2002), it could be that the ^{14}C date of the Charlotte Whale is even older than what was obtained here. Similarly problematic are the three dates obtained for the Daveluyville Whale. The date on the jaw of this specimen (MPEP717.2; UCIAMS 182298—11,930 ± 30 ^{14}C yr BP) is statistically significantly different from the other two, more recently obtained, dates. Further, these three new dates are statistically significantly different from the much earlier, non-AMS, date on this specimen (GSC-2871—11,400 ± 90 ^{14}C yr BP; Lowdon and Blake, 1981). Morphologically, the contrast of the fused epiphyseal plates in MPEP578.1 with the lack of fusion in the vertebrae of MPEP717 likely indicates that these specimens belong to two different individuals. Unfortunately, the ^{14}C dates and stable isotope data do not help in clarifying the number of individuals represented by the fossils. The δ^{13}C and δ^{15}N values are similar enough that they could derive from a single individual (Figure 2). However, the ^{14}C dates are more problematic in aiding in this interpretation. The new, replicate date of MPEP578.1 (UCIAMS 182297) is statistically significantly older than the previously obtained date of this same specimen (GSC-2871). Confusingly, this date is statistically similar to the date obtained on MPEP717.109 (UCIAMS-182296), but statistically significantly younger than the date obtained on MPEP717.2 (UCIAMS-182298). As mentioned above, especially for the three most recently obtained dates, the dates are close enough that they may not be meaningfully different with regards to when the Daveluyville Whale was last alive. If the significant differences are meaningful, these data would then hint at aberrant preservation of collagen in this specimen, effects of pretreatments such as conservation glue, and/or complications caused by marine reservoir effects on the ^{14}C values, for example.

Using the standard marine calibration curve (i.e., Marine20; Table 1), all three of these newest dates for the Daveluyville Whale calibrate outside the range or possibly just synchronous with the inception of the CS. With these specimens clearly coming from CS sediments, the calibration of the dates resulting in ages likely outside of the known range for the origin of the CS points to marine reservoir effects beyond the standard marine correction for the dated vertebrate specimens presented here, and as are common and long been known for the non-vertebrate fauna of the CS (Hillaire-Marcel 1988; Rodrigues 1988). Previous studies have shown marine reservoir effects and calculated offset corrections up to 1,780 ^{14}C years in the CS, but this is variable from locality to locality (Hillaire-Marcel 1988; Occhietti et al. 2001; Richard and Occhietti 2005; Rayburn et al. 2011). Interestingly, studies have also shown local marine reservoir offsets different from the average marine correction (about 400 years) in more recent Arctic marine ecosystems (Dyke et al. 1996; Furze et al. 2014). While offset corrections have been calculated for some CS localities, they should be utilized with caution, particularly when applying them to marine vertebrates. First, and in general for the CS, many of the offset corrections (ΔR) were determined using deposit feeding bivalve shells, which have been shown to present unpredictable offsets up to over 2000 years from sympatric suspension feeding bivalves (England et al. 2013). Second, and more specific to this study, ΔR is generally calculated using bivalves and plants, taxa that are not mobile. This study specifically analyzes taxa that are mobile, have large home ranges, possibly migrate in and out of the CS, and have diets of organisms (e.g., cod, capelin) that are also mobile (Dyke et al. 2019). For the species analyzed here it is difficult to reconcile what specific offset should be used even if there is a known ΔR calculated for a particular locality at a given time. For example, Richard and Occhietti (2005) present a terrestrial plant date along with a date on a foraminifera from the same level at Lake Hertel for which we can calculate a potentially appropriate ΔR. The ΔR from these samples, using the Marine20 calibration, is 900 ± 262 years. Calibration of the dates using this correction places the fauna examined here squarely within the chronology of the CS, although the effects of the correction uncertainty (i.e., 262 years) on the calibration does not help in addressing the timing of colonization (Table 1). That is, most of the calibrations range about 1500 years—about half the existence of the CS. Critically then, the accuracy and precision in the radiocarbon dates on CS vertebrate fossil specimens is limited because of the uncertainty related to ΔR. Therefore, the ^{14}C dates obtained in this and other studies on the CS marine vertebrate fauna may be influenced to varying degrees by localized marine reservoir effects (Harington 1977, 2003a; Feranec et al. 2014). Unfortunately, without knowing the marine reservoir offset for each specimen, we believe it is currently impossible to calculate the chronology of when particular species first colonized the CS. We provide these new ^{14}C dates with the hope that a reservoir correction and the chronology of vertebrate colonization can be calculated in future studies.

The stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope results are similar to those observed for the same species in modern arctic ecosystems (Hobson and Welch 1992; Hobson 1993; Dehn et al. 2007; Hansen et al. 2012; Marcoux et al. 2012), implying that they reflect the known ecology of the analyzed species. The carbon isotopes show a small, but seemingly typical, range in values for cold water marine ecosystems of the Northern Hemisphere (Hobson and Welch 1992; Hobson 1993; Dehn et al. 2007; Hansen et al. 2012; Marcoux et al. 2012). The δ^{15}N values show a much wider range indicative of individuals feeding at different trophic levels (Peterson and Fry 1987; Fry and Sherr 1989; Hobson and Welch 1992; Newsome et al. 2010).

Of the species studied here, the walruses, fin whale, and the right whale had the lowest δ^{15}N and δ^{13}C values. Modern fin whales (*Balaenoptera physalus*) have a diet heavy in krill (Borrell et al. 2012; Vighi et al. 2016; Aguilar and García-Vernet 2018). Taking the diet to bone δ^{15}N discrimination factor into account (~+2.0‰ for fin whales; Borrell et al., 2012), the average value obtained for the Daveluyville whale (+12.7‰) results in an expected krill value (+10.7‰) that fits within the range observed for different krill species in modern arctic ecosystems (Hobson and Welch 1992; Borrell et al. 2012; Hansen et al. 2012; Agersted et al. 2014; Vighi et al. 2016). Similarly, right whales (*Eubalaena glacialis*) feed exclusively on zooplankton, largely on copepods and krill, taxa having lower δ^{15}N and δ^{13}C values, such that we would expect right whales and fin whales to be isotopically similar (Fry and Sherr 1989; Hobson and Welch 1992; Hansen et al. 2012; Kenney 2018).

Similarly, for the walruses (*Odobenus rosmarus*), the δ^{15}N values are not unexpected as bivalve mollusks are a preferred food of this species in modern ecosystems. Being suspension or deposit feeders, bivalves occur lower on the food chain than most fish (Hobson and Welch 1992). Additionally, bivalves appear throughout CS sediments as species such as *Mya truncata*, *Macoma balthica*, and *Hiatella arctica* are regularly found in the sediments alongside the vertebrate fossil specimens (Thompson 1853; Harington and Sergeant 1972; Harington 1977, 1988; Lowdon and Blake 1981; Steadman et al. 1994). Interestingly, although walrus generally consume bivalves, they occasionally eat a variety of prey including fish and even seals and whales—prey at higher trophic levels (Fay 1982, 1985; Kastelein 2009).

Walruses, in general, forage for bivalves at depths of about 80 m or less, which would typically put them in more nearshore environments (Fay 1982, 1985; Born et al. 2003; Kastelein 2009; Jay et al. 2012). Additionally, many individuals utilize ice thick enough to support their weight as platforms to rest in between feeding excursions (Fay 1982; Jay et al. 2012). The availability of fast-ice or pack-ice is also supported by the presence of ringed seals (*Pusa hispida*) in the CS (Cournoyer et al. 2006; Feranec et al. 2014). As compared to the beluga whales in this study, the lower $\delta^{13}C$ values observed in walrus bone collagen could be due to the influence of glacial meltwater on the marine isotope values or simply the result of isotope values in prey taxa that occur lower on the food chain (Rau et al. 1983, 1989; Hobson and Welch 1992; Cronin et al. 2008; Hansen et al. 2012; Calleja et al. 2017). Further assessment of nearshore to offshore productivity is not possible to address as seasonal movements are not currently known for these CS species. Due to their foraging at depths expected nearer to shore, one might expect higher $\delta^{13}C$ values in walruses compared to the other analyzed species. However, the low $\delta^{13}C$ of walruses and fin whale in this dataset points to ecology and position in the food web as the primary factors controlling the observed values. An assessment of nearshore-offshore foraging on an individual level might be possible with serial sampling of walrus tusk fossils, for example.

As compared to the fin whale and the walruses, the thick-billed murre (*Uria lomvia*) and beluga whales (*Delphinapterus leucas*) had higher isotopic values. Today, the thick-billed murre, a relative of the now extinct Great Auk, regularly forages on capelin (*Mallotus*) and cod (*Gadus*) (Tuck 1961)—fish taxa that are also regularly found within CS sediments (McAllister et al. 1988). Similarity in isotopic values between the thick-billed murre and beluga whales is expected as belugas are also known to have a diet high in capelin and cod (Marcoux et al. 2012). The $\delta^{15}N$ and $\delta^{13}C$ values of capelin and cod are higher than those found in krill and bivalves, which can account for the differences observed in our dataset between the lower isotopic values of walruses, fin whale, and right whale and the higher isotopic values of thick-billed murre and belugas. Additionally, these isotopic values suggest that the individual species' ecology and ecosystem dynamics within the CS were very similar to those observed in modern arctic ecosystems.

Unfortunately, the inability to identify an appropriate ΔR to calibrate the ^{14}C dates for analyzed fauna makes the assessment of the effects of global climate change on the ecology of CS fauna impossible at present. It is worth noting however, that while global climate shows significant changes during the span of the CS, regionally the climate stayed colder (Anderson et al. 2007; Chapdelaine and Richard 2017). This fact may help explain why the ecosystem is isotopically similar to modern arctic ecosystems.

CONCLUSIONS

The Champlain Sea occurred in the St. Lawrence Lowlands of the northeastern USA and southeastern Canada from about 13,000 to 10,600 cal BP. Inception and termination of the CS was caused by isostatic depression and subsequent rebound of this area, a result of the weight and regression of the Laurentide Ice Sheet. This marine sea contained an abundant diversity of invertebrate and vertebrate fauna. Radiocarbon dates acquired on 15 CS vertebrate specimens imply the influence of varied marine reservoir effects on individuals, possibly relating to their mobility, and make it impossible to calculate the chronology of colonization for different species as well as the effects of global climatic change on species' ecology without knowing the specific marine reservoir offset corrections for each individual.

Stable isotope values in the CS are similar to those observed in modern arctic ecosystems implying similar ecosystem dynamics. Specific to this study, a fin whale, right whale, and walruses had lower $\delta^{15}N$ values indicating consumption of prey species from lower trophic levels, such as krill, copepods, and bivalve mollusks, as they do today. Additionally, the presence of walruses and ringed seals implies that fast-ice and/or pack-ice must have been available for hauling out. Higher δ^{13}C and δ^{15}N values observed in the belugas and thick-billed murre imply feeding on prey at higher trophic levels. Cod and capelin are likely prey for the belugas and thick-billed murre in the CS ecosystem. These fishes are prominent in their modern diets and they are regularly found as fossils in CS sediments.

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